Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

VOLUME XLVII NUMBER 2

BOTANICAL GAZETTE

FEBRUARY 1909

RELATION OF SOIL AND VEGETATION ON SANDY SEA SHORES

PEHR OLSSON-SEFFER

(WITH TWELVE FIGURES)

The studies on which the present paper is based were carried on during a number of years on a variety of sandy sea shores on the Baltic coasts, in Denmark, Holland, Scotland, and France, on the Mediterranean shores, along the coasts of Australia and New Zealand, in Hawaii, California, Mexico, and Central America.

In this paper I propose to give some of the observations made by myself regarding the conditions for plant life on coastal sand formations, and also to compare these investigations with the accumulated results from studies on this subject obtained by others.

Although considerable attention has been given to some of the most important points, I have as yet not been able to study in detail others, equally weighty; and in trying to interpret several of the phenomena of the distribution of sand vegetation I have found myself confronted with many problems, for the solution of which there is but little definite evidence at hand.

In discussing the factors that influence plant life, I have found it convenient to classify them into the following groups: atmospheric, hydrodynamic, edaphic, topographic, and historical factors.

To atmospheric factors all those are here referred, which directly influence the vegetation through the air. The atmospheric temperature, the light conditions, the variations in air moisture, the movements in the atmosphere, and the electricity are the principal factors of this kind. As hydrodynamic factors I understand all those connected with the water content of the substratum, and edaphic factors are

those relating to the chemical and physical quality of the soil. I call topographic those factors which have reference to the external features of the ground, and they affect indirectly more or less the factors belonging to previous groups. Historical factors are those which in the course of time exert an influence on the topography and thus indirectly on the plant covering.

Another series of factors analogous to the physical factors influencing plant life are the biotic. They are either zoobiotic or phytobiotic. Of the former especially the influence of man has to be recognized in connection with the study of vegetation on coastal sands. The phytobiotic factors are those caused by the plants themselves, and the mutual relationship of sand plants will be discussed in another paper.

Atmospheric factors

It is impossible to determine the relative importance of different factors influencing plant life, or to give one of these factors precedence in rank before another, because this depends in different cases on different conditions. It may be said, however, that the whole group of atmospheric factors is the most important, especially because of their influence on the transpiration of the plants. Sand vegetation is particularly affected by: (1) the large amount of heat absorbed by the sandy ground and reflected from its surface; (2) the intensity of illumination, both direct on the open, unprotected formation, and reflected from the white sand; (3) the exposure to winds, which constantly change the atmosphere.

TEMPERATURE.—If we compare in a general way the temperature conditions in a few of the localities under consideration, we find that there is no significant difference in results as regards development of sand formations or their vegetation in cold and warm countries. On the dunes along the Gulf of Finland, where the vegetation is in a dormant state for at least three months of the year, the sand drifts best during winter, when the grains are covered with a thin surface of ice, and are smooth. The friction is less and they are able to move slowly forward. The herbaceous vegetation is absent at this time, and the deciduous shrubs are without leaves. There is consequently nothing to arrest the movement of the sand.

On the Queensland coast, with a semitropical climate, the vegeta-

tion period extends over the whole year, but the sand drifts here much better during the summer, because winter is the rainy season, and when wet the coherence of the sand is greater. Plants like Ammophila, Cakile, Salsola, and Atriplex, of which the parts above ground die every winter on the Baltic coasts, grow all the year round on the shores of Australia, and there is no difference, external or internal, in structure. *Convolvulus soldanella* on the coast of Holland does not differ from the same species on the shores of tropical countries, where it is common (*fig. 10*).

Dunes are formed in warm countries more generally than in cold because of the longer periods of drought, which favor the drifting of the sand. We refer to the enormous areas of sand formations in Africa, both on the coasts and in the interior, in the deserts of Asia, on the coasts of India and Australia, in the interior of the latter continent, on numerous tropical coasts as Java, Hawaii, etc. The dunes which occur in really cold countries, as in certain parts of the United States and northern Europe, are insignificant in comparison with the former.

It would be of considerable interest to have correct data of temperature conditions from the various localities where the author has made his studies of the coastal sands. The field-work on which this paper is based, however, has been conducted for comparatively short periods at each place, and the temperature observations made do not offer, therefore, any reliable basis for comparisons. Official data, obtained from meteorological stations on the coasts, are also unsatisfactory for our special purpose, because the instruments usually are kept close to buildings, away from vegetation, in more or less sheltered positions, and because of these facts the observations cannot serve for any definite conclusions as to the real temperature conditions under which the vegetation has developed. It is not necessary to burden these pages with computations of any general data of the kind referred to. The author has compared a great number of temperature statistics from different coasts, but he has entirely failed to find any apparent rules applicable to the development in general of sand vegetation in different climates. This negative result is not due to absence of such laws, which certainly must exist. It merely shows that our knowledge is deficient and the present method of taking temperatures at meteoro-

logical stations is entirely inapplicable to the subject under consideration.

For ecological purposes temperature observations in the field have to be made very carefully if we are to draw from them any conclusions of value as to the influence of heat on the vegetation. And further, they have to be extended over a long period of years before we are justified in advancing any general laws of temperature influence on distribution of plants.

Let us here draw attention to the opinion held on this question by the greatest authority on ecology, Professor WARMING. In his renowned handbook on ecological phytogeography (**14**) he says on page 22, speaking of the many attempts to determine the sum-totals of temperature in relation to geographical distribution, that these investigations need in a very high degree to be supported by really scientific experimental determinations of the cardinal temperatures for the phenomena of different species. And even the results of such observations would hardly be sufficient for the solution of the very difficult and complicated questions of the importance of heat conditions for distribution of species and phenological phenomena, as other factors, perhaps, to some extent can replace a higher temperature.

One feature of the heat conditions on coastal sands is apparent. That is the great fluctuation of diurnal temperatures. On account of the low specific heat of sandy soil, the surface layers are rapidly heated by the sun in daytime and as quickly cooled by night. These variations of temperature are conducted by radiation to the lower strata of the atmosphere, or those in direct touch with the plants, which consequently are greatly affected by such changes.

Of some occasional observations by the writer on the diurnal range of temperature on sand dunes the following may be mentioned as examples of the great divergence between temperature extremes in such localities.

Observation 64.—Dunes at Hangö, Finland, September 10, 1897. Maximum temperature in the shade (thermometer from unknown maker) 28°.8 C., between 6 A. M. and 6 P. M. Minimum (thermometer from WALLMANN in Stockholm) 2°.6 between 6 P. M. and 6 A. M. Range 25°.6. The instruments were placed on an open sand surface 25^{cm} above the ground, and were shaded by white canvas, 2^{m} high. Ordinary thermometer readings in the shade were taken every hour in the daytime, giving the following results:

6 A. M.	8°.5 C.	10 A. M.	14° C.	2 P. M.	23°.6 C.
7 A. M.	9.2	11 A. M.	17	3 P. M.	27.2
8 A. M.	9.8	12 M.	19.4	4 P. M.	27.5
9 A. M.	11.4	1 P. M.	20.6	5 P. M.	22.4
				6 P. M.	15.9

This place of observation was on an open spot, unprotected from the winds. About 60^{m} inland between the pines, and sheltered from winds, the thermometer gave 7°.4 C. at 6 A. M., 9°.2 C. at 9 A. M., 16°.6 C. at noon, 28° C. at 3 P. M., 16°.2 C. at 6 P. M. This shows that the temperature was slower to rise in the morning and forenoon, but once high it was also slower to decrease, when the energy of the solar rays was diminishing toward evening.

Observation 576.—Dunes at North Beach, near Perth, Western Australia, September 12, 1902. Maximum in the shade 31°.1 C. (8 A. M.–6 P. M.). Minimum 6°.8 C. (6 P. M.–8 A. M.). Range 24°.3. The instruments, from NEGRETTI & ZAMBRA in London, were elevated 30^{cm} above ground and shaded by a white canvas tent with open sides. The hourly variation was the following:

8 A. M.	7°.9 C.	12 M.	23°.6 C.	4 P. M.	19°.5 C.
9 A. M.	11.2	1 P. M.	29.4	5 P. M.	16.3
10 A. M.	15.6	2 P. M.	30.7	6 P. M.	9.6
11 A. M.	18.6	3 P. M.	20.3		

These data show, as in the previous observation, that the temperature rose steadily until about 2 P. M., although the rise is so much more rapid in these latitudes on account of the greater energy of the sun. In this case, however, over 10° in a single hour, and nearly 10° more between 4 and 6 P. M.

On the coast of Western Australia a sea breeze always sets in about noon, according to COOKE (4), the temperature then begins to fall until evening, and the nights are generally cool the whole year round.

The influence on vegetation of such a wide range of temperatures must necessarily be of considerable importance. Although these air temperatures have been largely affected by radiation, the direct radiant heat of the sun is still more important. Actinometric methods of registering intensity of solar radiation are, as yet, very unsatisfactory. Almost the only instrument available for field observations is the so-called black-bulb thermometer *in vacuo*. The rather casual observations of this kind made by the writer will be referred to in another place in connection with some transpiration phenomena. It may suffice, however, to say here that these occasionally taken measurements, in spite of their discontinuity, have convinced the writer that the surest and most effective way of attacking the problems of heat influence on vegetation is to pursue investigations on the lines of actinometric records. Neither the mean temperature of the air nor the sum-total of atmospheric temperature is of such importance

to vegetation as the amount of direct solar radiation and radiation of heat from the ground. The value of the former factor in climatology has long been recognized by meteorologists.

We must never lose sight of the fact, however, that it is not one factor alone that determines the development and distribution of the vegetation, but a resultant of the many different conditions to which the plants are subjected. This has been duly emphasized by WARMING (14).

LIGHT.—In the closest relation to atmospheric temperature, and especially to radiation of heat, is the factor of light. The intensity of illumination is remarkably large on the open sand formations of the coast, and this circumstance is noticeable in the many protective adaptations of plant structures against the influence of light. There are as yet no reliable means of ascertaining the intensity of the light, and we have consequently no basis for comparisons on this subject. The strong insolation on the white surface of the sand favors a greater variation of temperatures than on other formations of the coast. The radiation is, however, generally less on the coast than in localities far away from the sea because the larger quantity of aqueous vapor in the atmosphere in the former place tends to check this terrestrial radiation.

HYDROMETEORIC CONDITIONS.—This term has here been used to distinguish the factors of atmospheric humidity from those of the water content of the soil or the substratum from which the plants take their supply. On coastal sands it is perhaps more apparent than on other formations that there is some difference in influence and effect on vegetation of the moisture contained in the air and of the water in the soil. It is, however, always extremely difficult to decide to what extent certain adaptations are due to one factor more than to another, especially when we do not possess detailed observations.

AIR MOISTURE AND EVAPORATION CAPACITY.—The supply of atmospheric moisture is to a great extent obtained from the ocean, and it follows that on the coast the amount of humidity must be much greater than farther inland. This is in fact an everyday observation.

We do not know for certain to what extent the plant is able to condense water vapor and absorb atmospheric humidity, but we do know that moisture in the air greatly lessens transpiration, and, other factors being equal, transpiration ought therefore to be less on sea shores than

inland. Now it is not the absolute humidity that determines the amount of evaporation, but the saturation deficit or the amount of water which the atmosphere at a certain temperature is able to absorb (WARMING). In the continental interiors the evaporating power of the climate is very great during summer, and on account of the cold quite inconsiderable during winter (HANN **7**). If we compare the habits of certain plants which occur both in the interior deserts, and on coastal sands we shall find them instructive. For instance *Mesembryanthemum aequilaterale* has the same appearance when growing on the beach or in the immediate neighborhood thereof, as when occurring on the interior sands of Australia, many hundreds of miles from the coast. But when found at a certain distance, 0.5^{km} or so, from the beach, *outside the influence of the spray from the sea, and sheltered from the full force of the ocean*, it grows higher, its leaves are two or three times as long, and its succulence is less marked than in specimens from the beach or from the interior. In the case of the writer's observation, the places of growth were as nearly similar as possible with regard to exposure to the rays of the sun and moisture in the soil. Some notable differences in anatomical characters observed in this connection will be alluded to in another paper. These characters also proved that the devices for protection against excessive transpiration were not so well developed in the specimens which were not exposed to the strong salt-laden winds, although they had the full benefit of the coastal moisture.

If we may be allowed to draw any inferences from this fact, we should conclude that, as a rule, *transpiration is less on coastal than on interior sands*. There are other factors, however, to be taken into consideration, which somewhat equalize the conditions, as the wind and the salinity of the atmospheric moisture.

Everywhere on warm coasts, especially in the neighborhood of the sea, on the beach, we can notice a peculiar sand flora. It is characterized by species which do not occur farther inland, and on the other hand inland plants as a rule do not go down to the beach. The greatest part of this strand flora consists of halophytes or plants growing in salty situations.

It is generally assumed that the conditions in which halophytes thrive are dependent on the amount of salt present in the soil. As

we shall show, when speaking of the edaphic factors, the quantity of salt present in the soil in some of the coast formations is quite inconsiderable, but still the plants exhibit the same characters typical of those which grow where salt occurs in the soil.

We cannot here escape the conclusion that the influence which is exerted on the plants in one case by the salt-water content in the soil, in the other case is brought about by some other cause of similar kind.

Analysis of spray from the sea reveals the presence of a large amount of salt, usually even more than in the sea water, because water is evaporating from the drops of spray and the fine particles of moisture near the ocean. This salinity of the spray is greater at a high temperature, as the evaporation is then more intense, and it is common to find on hot days, with sea wind carrying moisture landward, that salt is deposited in form of crystals on the plants and on other objects, as well as on the ground.

A few analyses will be given to illustrate this large quantity of salt in the atmosphere on the sea coast. In all instances when samples of spray were secured, the method was as follows. Pieces of muslin, thoroughly examined and found free from salts, were dried and kept in tight-closed jars until exposed at the place were the sample was to be taken. The muslin was then exposed to the sea spray; the temperature and time of exposure were registered, the muslin bottled, and later examined in the laboratory. At the same time samples of the sea water were secured for chemical analysis. The following results were obtained from four observations:

I. Nagu, Högsar, Finland, August 22, 1897. Atmospheric temperature 19°5 C. Sky clear. Velocity of wind about 7^m a second. Muslin exposed for 1^h 15^m, at a distance of 9^m from the water. Salinity of spray sample 0.673 per cent., of sea water 0.662 by areometric measurement, and 0.632 per cent. by chemical analysis. Temperature of water 15°0 C. As is the case in this observation the areometric value of salinity is always somewhat higher than that obtained by analysis.

II. Hangö Tulludd, Finland, September 9, 1897. Atmospheric temperature 21°2 C. Sky partly overcast. Velocity of offshore wind about 10^m a second. Muslin exposed on the beach, 5^m from water, for 2^h. Salinity of spray sample 0.625 per cent., of sea water 0.607. Water temperature 13°6 C.

III. North Beach, near Perth, Western Australia, September 16, 1902. Atmospheric temperature 24°6 C. Sky clear. Velocity of wind, measured with anemometer (of Crova type, from NEGRETTI & ZAMBRA, London) averaging 12.3^m a second during time of observation. Muslin exposed on the beach, 8^m from the water, for 4^h 15^m. Salinity of spray 4.68 per cent., of sea water 3.24 per cent. Temperature at the surface 10°6 C.

IV. Beach at Pialba, Queensland, on the eastern coast of Australia, June 17, 1901. Atmospheric temperature 16° C. Sky clear. Velocity of wind about 6^m a second. Muslin exposed 5^m from the water. A heavy surf was rolling at the time, but as the water is shallow far out from shore, and sheltered by clumps of mangrove, the breakers did not strike the shore with any force. The sample showed a salt content of 4.1 per cent. Salinity of ocean water 2.91 per cent., and temperature 9°4 C.

Although the presence of sodium and chlorine, as common salt, can be shown in many inland plants, a larger percentage of these salts is found in the ash of strand and marine plants than in that of the former type.

Whether these salts are absolutely essential for any plant we do not know for certain. If that is the case, the amount of salt needed is very small, as has been shown by several investigators. Even for many marine algae only the smallest quantities of salt are necessary, if at all essential.

Inland plants are, however, unfavorably influenced by a percentage of salt which strand plants bear without injury; on the other hand, it has been proved by cultures, that the halophytes can grow without the usual amount of salt contained in the soil or atmosphere of their natural habitat.

An interesting experimental study of strand and other plants with relation to common salt and sea water has been made by COUPIN (**5**). He found that 1.5 per cent. of common salt in soil or in water is poisonous to plants which do not naturally grow on the sea shore. Sea water contains about 2.5 per cent. of common salt, and the soil washed by the sea, as well as the atmosphere near the coast, contains still more than this proportion. We can thus readily understand the sharp line which separates the marine and strand floras from those of the interior. COUPIN attributes the poisonous property of sea water for inland plants mainly to its content of common salt, for the two salts next to this in abundance, magnesium sulfate and magnesium chlorid, are present in quantities which he considers below the toxic proportions. Magnesic sulfate is poisonous at a concentration of 1 per cent., magnesic chlorid at 0.85 per cent., but they occur in sea water only to the extent of 0.75 per cent. and 0.5 per cent. respectively.

The question of the influence of salt on strand plants and of the

absorption by the plant of saline water has been discussed considerably, and several theories have been advanced.

PRECIPITATION is a factor, which on naturally dry soil, such as presented by sand formations, is of considerable importance, not only on account of the quantity of water which in this way is brought to the plants, but also because of its influence in giving coherence to the sand, thus preventing it from shifting, and because of its weathering action on the soil particles.

That precipitation must to a great extent influence the development of vegetation on marine coasts is evident, and it is easily seen that the composition of the plant covering of sand formations varies somewhat in rainy and rainless climates, although the atmospheric humidity on the coast tends to minimize this difference. The latter factor is especially important as the precipitation often is so variable. The absolute amount of rain during the year does not in fact give any correct basis for comparison of the conditions in different localities, as it is far more important for the vegetation how this quantity is distributed over the period in question. On the Baltic shores the number of rainy days of the vegetative season is much greater than, for instance, on the coast of Australia or California. The eastern coast of Australia, at Brisbane, has an average yearly rainfall of 129.5^{cm} while the Åland Islands in the Baltic have only 52.9^{cm}, but the vegetation in the latter region has a much more even supply of moisture during the vegetative season, because the precipitation is distributed over a greater number of days, about 70 of the 160 rainy days of the year falling in the growing season.

Edaphic factors

When SCHIMPER proposed this term (1898) he apparently regarded it as covering all the peculiarities of the ground. It seems to the present writer that it would be more convenient in this connection to distinguish between the soil as such, and the media, water and air, filling the interstitial spaces. This distinction has been made in this paper by separating the factor of soil moisture under the heading *hydrodynamic*, and the factors pertaining to the soil proper as *edaphic*.

The hydrodynamic factors are now generally admitted to be of the very greatest importance for the vegetation and its distribution. I

have treated this subject in another place (12). With regard to the edaphic factors, *sensu scriptoris*, a wide difference of opinion has prevailed. While some writers have maintained that the chemical influence of the soil is the most important, others have been in favor of the theory which gives to the physical properties of the soil the largest bearing. Since the physical conditions mainly determine the amount of water, most recent authors upon the subject, among them WARMING, hold that these are of greater consequence.

In discussing the physical conditions of sand formations we will confine ourselves to the question of soil temperatures, and further briefly refer to some measurements of the size of sand grains made by the writer.

SOIL TEMPERATURE.—The heat-absorbing power of sand is low in comparison with other darker-colored soils, but because the radiation is great the vegetation on a surface of sand is subjected to a comparatively high temperature. As the sand is always moist only a little below the surface the heated layer of sand does not reach deep before it meets lower temperature.

The roots always penetrate to this moist layer, and only the upper part of the root is under the influence of the heat of the surface stratum of sand. We find corresponding adaptational protections on the roots of most plants growing in sandy soils.

The transport of heat within the soil is influenced by several factors outside the conductivity from one layer to another. It is impossible, however, in the natural state of the soil to eliminate these factors, the movements of water and air in the soil, the evaporation of water from the warmer and condensation of water vapor in the colder strata. The data here supplied therefore represent the temperature of the soil under conditions such as it presents in the field.

In all observations made by the author ordinary soil thermometers were used, and the temperature was taken at following depths: 2, 5, 10, 20, and 50^{cm}. The bulb of the instrument can easily be placed in loose sand at the desired depth. The number of complete series of observations made on different sand formations reaches 876. Some of these will here be referred to, and in other cases average values will be given.

On the front beach the temperature of the soil is varying more

than on other formations of the sand strand, because of the frequent inundations and subsequent changes in evaporation. It is generally low as compared with that on the higher parts of the beach. Seven measurements taken at Högsar, Nagu, Finnish Archipelago, in June, 1894, averaged 16°.4 at a depth of 2^{cm}. The corresponding data, obtained at varying depths, are shown by Table I.

TABLE I

	2 cm.	5 cm.	10 cm.	Air	Sea water	Time	Wind velocity, m. per sec.	Cloudiness 1–10
1	18.3	16.3	17.4	19.6	18.4	12:30 P. M.	1.5	2
2	14.9	15.5	16.3	13.8	16.6	2:00 P. M.	0.5	6
3	19.6	18.9	18.6	19.8	16.7	11:30 A. M.	4.1	4
4	16.5	15.8	15.9	16.5	16.9	2:00 P. M.	0.3	0
5	14.2	14.6	15.2	14.4	16.5	1:30 P. M.	2.6	1.5
6	13.3	13.6	12.9	14.0	15.6	1:30 P. M.	1.8	2
7	16.7	15.4	14.7	16.9	16.5	2:00 P. M.	0.4	1

In all cases except 3 the sand was covered with vegetation, in 5 and 7 with *Glaux maritima*, in 2 with *Erythraea litoralis*, in 1 and 4 with *Argentina anserina*, and in 6 with *Triglochin maritimum* and *Eleocharis uniglumis*.

In September, 1902, similar measurements were taken on the front beach at Freemantle, Western Australia. No vegetation occurred on the formation. The following results were obtained (Table II):

TABLE II

	2 cm.	5 cm.	10 cm.	20 cm.	Air	Sea water	Time	Wind velocity, m. per sec.	Cloudiness 1–10
1	32.6	25.4	22.9	20.2	26.4	13.4	9:00 A. M.	2	1
2	37.4	28.7	27.1	24.9	30.1	14.6	1:00 P. M.	2	1.5
3	26.2	19.2	17.4	15.6	27.5	12.9	2:00 P. M.	1.5	3
4	25.4	20.4	18.5	15.8	24.4	12.5	11:30 A. M.	0.3	6
5	21.3	15.6	14.2	13.6	22.7	12.8	12.15 P. M.	3.5	4

The average temperature of these five series at 2^{cm} depth is thus 28°.5 C., that is, 12°.1 higher than the mean of the previous series. The sea water in the latter case was much colder, while the atmospheric temperature was considerably higher.

Of sixty measurements taken in day time on the front beach under conditions as similar as possible, the highest temperature obtained for 2^{cm} depth was 42°.6 C. on the Queensland coast at Pialba, in Decem-

ber, 1901, while the lowest was 2°.1 near Mariehamn, Finland, in September, 1896. The average of these sixty observations was 18°.4 C.

The soil temperature on the middle beach is already much higher, as following data will show. The observations were made at the same time and in the same place as those mentioned in Table I. The distance from the water was 6.5^{m} and the sand pure quartz of medium size and yellow color.

TABLE III

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1............	22.6	20.1	17.8	14.1	12.6
2............	19.1	16.7	14.9	12.7	12.1
3............	23.4	21.3	18.9	15.3	13.3
4............	20.1	18.5	17.0	13.9	12.7
5............	18.4	16.9	15.6	12.7	12.2
6............	16.9	15.2	13.7	12.6	11.9
7............	19.8	17.3	15.5	13.8	12.9

The vegetation consisted in 1 and 3 of an open community of the following constituents:

FACIES: *Leontodon autumnale*, copious.

SECONDARY: *Festuca rubra arenaria*, subcopious, *Agrostis vulgaris*, subcopious, *Plantago maritima*, gregarious, *Erythraea litoralis*, sparse.

In 2 Erythraea was scattered about in patches, between low shrubby *Alnus glutinosa*, solitary individuals of *Elymus arenarius*, and *Rosa canina*.

In 4, 5, and 7 a *Juncus Gerardi* community occurred on the middle beach, with sparse *Erythraea litoralis* and *Plantago maritima*. In 6 *Elymus arenarius* and *Festuca rubra arenaria* formed an open community.

A parallel table to Table II shows the temperature conditions on the middle beach at Fremantle, W. Australia. The sand was here fine, consisting of pure light-yellow quartz. Time and atmospheric conditions as in II.

TABLE IV

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1............	35.2	23.4	22.4	20.7	18.4
2............	38.6	25.8	24.6	23.6	20.0
3............	29.5	18.6	18.3	16.5	15.8
4............	27.2	21.3	19.6	17.2	16.3
5............	24.6	16.9	16.1	14.9	14.4

A comparison with the results in Tables I, II, and III reveals the fact that, while the surface temperature (2^{cm}) in all cases was higher in the series given in Table IV than in Table II, the temperatures at 5^{cm} and lower were higher in the former case, presumably on account of a more intense evaporation, which caused a corresponding loss of heat. No such difference existed between Tables I and III, where the solar radiation was less, and both the atmospheric and sea-water temperature lower.

We shall now proceed to a statement of the temperature conditions on the upper beach. Table V gives the results of some observations made on that formation at Jerwe on the Oesel Island in the Baltic, in July, 1896. The beach has a low grade and is limited landward by a littoral dune in the shape of a steep and high bank, on the top of which small dunes are developed. The sand on the upper beach at the foot of this bank is rather coarse, consisting of a reddish-yellow quartz.

TABLE V

	2 cm.	5 cm.	10 cm.	20 cm.	Air	Sea water	Time	Wind velocity, m. per sec.	Cloudiness
1 . . .	22.4	22.8	21.4	19.6	21.6	17.1	10:30 A. M.	1	3
2 . . .	27.3	26.2	24.5	22.7	25.2	16.4	1:00 P. M.	0.5	1
3 . . .	26.8	24.3	22.8	21.1	23.6	16.1	3:15 P. M.	2	5

The next table is a continuation of the measurements given in Tables II and IV from Fremantle, W. Australia, and the general conditions supplied in regard to those tables refer also to these observations on the upper beach, except that the time in each case was about 15 minutes later. The sand was of medium-sized, white-yellow quartz, mixed with an abundance of shell fragments.

TABLE VI

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1	34.8	24.5	22.6	21.1	18.3
2	38.9	24.9	23.4	22.0	19.6
3	28.8	19.2	17.6	16.4	14.8
4	27.6	22.5	20.7	18.2	16.6
5	25.3	17.3	16.9	14.5	13.8

As will be seen, the temperature on this formation does not differ

essentially from that on the middle beach at the same locality as given in Table IV. The differences existing may be accounted for by the topography and by the fact that the upper beach here was covered with a sparse vegetation consisting of various low herbs.

On the littoral dune the temperature conditions are somewhat varying, usually higher on the landward slope, and a rise in temperature can also be noticed with an increase in the height of the dune. The summit and the landward slope of the littoral dune are frequently covered in large patches with vegetation, and the temperature differences between the open spots and those where plants occur are considerable.

Table VII shows a series of measurements made on the seaward slope of the littoral dune at Fremantle, W. A., under conditions similar to those given for previous observations from that locality. The sand was fine white quartz.

TABLE VII

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1	35.2	26.4	23.5	21.5	19.2
2	38.8	27.3	22.6	20.6	18.4
3	29.4	20.5	18.1	16.2	15.4
4	28.9	21.3	19.4	17.7	16.2
5	25.6	18.7	16.6	15.1	14.3

Table VIII gives the temperature on the summit of the same dune, at a height of 6^m over the ocean level. The dune material consisted of medium sand, somewhat yellowish in color.

TABLE VIII

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1	35.5	27.4	24.2	21.7	19.8
2	38.8	28.1	23.0	21.2	18.9
3	30.3	21.0	18.2	16.8	15.7
4	30.1	21.8	18.9	18.3	16.3
5	26.4	18.8	16.7	15.7	14.0

On the landward slope, some 3^m from the top, the following measurements were obtained:

TABLE IX

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1	35.4	27.0	23.6	21.5	19.4
2	39.2	27.6	22.8	20.4	18.2
3	29.8	20.8	18.1	16.5	15.6
4	29.5	21.7	19.0	17.8	16.1
5	25.9	18.9	16.8	15.6	14.3

In this last case the sand was rather fine quartz, of yellowish color. The maximum soil temperature measured by the author on a littoral dune formation was obtained in December, 1901, on the leeward slope of a high dune at Southport, Queensland, where the thermometer 2^{cm} under the surface registered 58°4 C. at 2 P. M. The formation was devoid of vegetation.

The temperature of the dunes and the sand fields varies greatly. Some averages will be here given. Of the 34 readings made under general conditions as similar as possible a mean temperature of 26°2 C. was obtained from dunes in Finland for a depth of 2^{cm} and 25°4 for 5^{cm}. The average of 19 readings at Fremantle, W. A., was 28°7 C. and of 12 readings at Southport, Queensland, 29°8. On the dunes of North Cape, New Zealand, the author measured on the same day within one hour the following series: 26.1, 25.8, 24.2, 27.9, 25.4, 26.3, 26.1, 27°9 C. The atmospheric temperature at the time was 25°4, cloudiness 3, time December 7, 1902, 11:30 A. M.–12:30 P. M.

The daily variation of temperature must naturally be of some importance to the vegetation. Only a few observations have been made by the writer to this end. One series will be given as a sample of the extent to which such variations take place. The readings were made at Southport, Queensland, in December, 1901.

In the light of measurements obtained the local distribution of certain plants on the coastal sand formations seems to indicate that the temperature factor is of the greatest importance for the mode of association of plants into communities. On the coasts of the Baltic the writer made frequent observations which tend to show this.

At Åhus in Sweden there occurs on the upper beach an Ammophila-Elymus community, consisting of the following plants:

FACIES: *Ammophila arenaria, Elymus arenarius.*

SECONDARY: *Triticum junceum, Carex arenaria, Festuca rubra arenaria, F. ovina, Poa pratensis, Cakile maritima, Halianthus peploides.*

TABLE X

HOUR OF READING	ATMOSPHERIC TEMPERATURE	DEPTH UNDER SURFACE					CLOUDINESS 1–10
		2 cm.	5 cm.	10 cm.	20 cm.	50 cm.	
6 A. M......	9°6 C.	4.9	4.2	5.7	9.1	14.3	6
7	10.8	6.5	5.6	5.9	9.4	14.4	2
8	11.4	7.7	6.9	6.2	9.4	14.6	3
9	15.6	9.0	8.9	6.9	9.6	14.6	1.5
10	17.7	11.2	10.2	8.0	9.7	14.5	4
11	19.5	14.6	11.8	9.6	9.8	14.5	3
12 NOON	23.2	17.2	13.0	10.5	10.1	14.7	3
1 P. M......	26.3	19.6	14.3	11.8	10.7	14.4	5
2	27.2	19.4	14.8	12.6	11.4	14.5	4
3	27.0	18.1	14.6	12.7	11.6	14.5	4
4	26.4	18.0	14.3	12.6	11.8	14.4	5
5	25.1	17.3	14.0	11.8	11.6	14.5	4
6	22.3	15.1	13.5	11.2	11.7	14.6	2.5
7	18.6	12.9	12.3	10.4	11.9	14.6	1
8	16.2	11.0	10.7	9.5	11.6	14.7	0.5

The two species which constitute the facies of this community usually occur in small separated patches, and measurements of the temperature in the small sand elevations formed by these plants revealed the fact that in the Ammophila patches the soil temperature almost invariably was two-tenths to six-tenths of a degree higher that in the latter case, which would explain the lower temperature, but the exact difference in moisture has not been ascertained. Many similar instances of temperature differences have been noticed. *Halianthus peploides* always grows in colder places than *Argentina anserina,* although both together often form a community. This question of temperature differences influencing the formation of communities, however, needs further investigation before any decisive statements can be made. It must also be remembered that the temperature is influenced by the moisture, which in its turn depends to a great extent on the physical conditions of the soil.

MECHANICAL ANALYSIS OF SAND.—A considerable number of such analyses have been made by the writer, and a few series will here be given to show approximately the differences in size of sand grains on the various formations on different sand strands. In the table the

letter *A* refers to a series of samples from Kurische Nehrung on the northern coast of Germany, *D* to a series from sand formations near Amsterdam in Holland, *E* to sand from the west coast of France south of Bordeaux, *F* to samples from the west coast of Australia, near Fremantle, *G* to sand from Port Fairy, Victoria, *H* to the sand at Southport, Queensland, *I* to a series from North Cape of New Zealand, and *J* to a series of samples from the Pacific coast of North America near San Francisco.

	A	B	C	D	E
Submerged beach	Finest	Medium	Medium	Fine	Finest
Front beach	Fine	Medium	Fine	Fine	Coarse
Middle beach	Fine	Fine	Coarse	Medium	Coarse
Upper beach	Coarse	Medium	Coarse	Medium	Grits
Littoral dune	Medium	Fine	Medium	Fine	Medium
Dunes	Medium		Medium	Fine	Medium
Sand field		Finest			Finest

	F	G	H	I	J
Submerged beach	Coarse	Medium	Fine	Coarse	Medium
Front beach	Medium	Fine	Medium	Grits	Fine
Middle beach	Medium	Medium	Coarse	Coarse	Fine
Upper beach	Coarse	Medium	Coarse	Grits	Medium
Littoral dune	Medium	Fine	Medium	Medium	Fine
Dunes	Fine	Fine	Medium	Fine	Fine
Sand field		Finest			

In each of the above cases the result represents the average of 10 samples, secured at approximately corresponding places on each formation. As these data show, the coarsest sand occurs on the upper beach. The material that builds up the littoral as well as the ordinary dunes is usually of the same grade of coarseness. It is only when we analyze the sand from various places on the dunes that differences appear, which explain the formation of ripple marks and dunes as discussed on previous pages. It will be seen when we describe the vegetation on the various formations that the coarseness of the sand in some cases seems to determine the composition of the plant communities. This is easily understood when we consider that the size of the sand particles determines the water-holding capacity of the soil.

CHEMICAL COMPOSITION OF SAND.—The nutritive value of sand is different according to the chemical character of the sand grains. As

a rule, sand is very deficient in plant food, and this is especially the case with the commonest form of sand, that which consists mainly of quartz. The quartz grains are insoluble, or only to a very small degree soluble. Only in the case of lime or organic matter in the form of humus entering into the composition of the sand is there plant food in sufficient quantities to allow the development of a more luxuriant vegetation. Generally the chemical composition of coastal sands is very uniform, and this may to some extent account for the evident similarity in vegetation on these formations.

A number of analyses of sand have been made by the writer, and some typical results will be here related.

No. 1.—Middle beach, Eckerö Storby, Åland Islands, Baltic

	Per cent.		Per cent.
Insoluble matter	89.25	Alumina	1.38
Soluble silica	3.44	Water and organic matter	2.57
Lime	1.06	Nitrogen	0.16
Potash	0.18	Other constitutents	1.02
Phosphoric acid (soluble)	0.24	Total	100.01
Peroxid of iron	0.71		

No. 2.—Littoral dune, Engelholmshamn, Skåne, S. W. Sweden

	Per cent.		Per cent.
Insoluble matter	84.38	Alumina	1.83
Soluble silica	4.53	Water and organic matter	4.93
Lime	1.04	Nitrogen	0.12
Potash	0.21	Other constitutents	2.00
Phosphoric acid (soluble)	0.33	Total	99.99
Peroxid of iron	0.62		

No. 3.—Upper beach, North beach, near Perth, W. Austr.

	Per cent.		Per cent.
Insoluble matter	86.32	Alumina	0.93
Soluble silica	3.61	Water and organic matter	2.89
Lime	1.53	Nitrogen	0.03
Potash	0.36	Other constitutents	3.33
Phosphoric acid (soluble)	0.15	Total	100.02
Peroxid of iron	0.87		

No. 4.—Dunes, Southport, Queensland

	Per cent.		Per cent.
Insoluble matter	91.90	Alumina	1.08
Soluble silica	3.18	Water and organic matter	2.15
Lime	0.86	Nitrogen	0.11
Potash	0.21	Other constitutents	0.44
Phosphoric acid (soluble)	0.29	Total	100.00
Peroxid of iron	0.08		

No. 5.—DUNES, GOLDEN GATE PARK, SAN FRANCISCO, CAL.

	Per cent.		Per cent.
Insoluble matter	88.27	Alumina	1.08
Soluble silica	4.42	Water and organic matter	2.15
Lime	1.94	Nitrogen	0.05
Potash	0.17	Other constitutents	1.80
Phosphoric acid (soluble)	0.08	Total	100.01
Peroxid of iron	0.05		

These analyses show what a small amount of plant food is available in the dunes in comparison with that in ordinary agricultural soil, where the insoluble substances do not comprise more than 70 per cent. of the total volume. And it must be remarked that the analyses here given represent soil from places more or less covered with vegetation, where the organic constituents are better preserved from decomposition and from being washed out by water than on open sand. They therefore show a higher percentage of humus and soluble material than the barren quartz unprotected from the influence of sun, air, and water. Where sand has recently been deposited after having been exposed for some time to sea water it is naturally very deficient in plant food, and it has therefore to be considerably changed before it is able to sustain a vegetation covering.

The amount of lime contained in the dunes varies to a great extent. On tropical coasts it is generally very large, especially where the sand is formed by disintegration of coral rocks. On such shores carbonate of lime is dissolved by the rain water and the sand is at a low depth under the surface consolidated into limestone. A similar process of calcification can be observed also on many coasts where the amount of lime is quite small, as on some coasts of Europe. BANG (1) has observed that the dune sand near the sea contains up to sixteen times more lime than farther inland. This is a natural result of the washing-out process and decomposition, which takes place on the open sand, and is more effective farther inland, because the supply diminishes with the distance from shore.

On the upper beach and on the seaward slope of the littoral dune are frequently found fragments of shells that have been carried ashore by the waves. In places where the littoral dune is broken, shells are often accumulated in the depressions, while more landward the lime in the animal remains is disintegrated by the carbon dioxid of the rain water.

The greater or smaller amount of peroxid of iron in dune sand determines to some extent its color. The usually colorless grains of pure quartz are covered with a thin coat of ferric hydroxid, which gives the sand its yellow color, and in some places almost a red tint.

THE SOLUBLE SALT CONTENT IN COASTAL SAND.—Of the soluble salts that saturate the coastal sands sodium chlorid is the most important. Its presence, as common salt, in all plants is well known, and its influence on the littoral flora is very apparent. Whether sodium chlorid is essential to plant life is still an open question, and the investigations hitherto conducted in order to ascertain this fact seem to indicate that such is not the case. In experiments it is difficult to eliminate salt entirely, but it has been conclusively shown that the smallest quantities only, if any at all, are needed for the development of plants, even for those which apparently prefer salty situations, when growing under natural conditions.

That common salt is injurious to plants, when present in excessive quantities, is certain. It is commonly believed that this unfavorable influence of salt is due to the amount of magnesium chlorid it contains. It is more likely, however, that all the chlorids are injurious, and experiments by the writer have supported this view, previously maintained by several authors.

It is generally stated by various writers that the formations on the sea coast contain a considerable amount of common salt. Thus WARMING (**14**) says that on the sandy beach the salty ground water is found at only a slight depth under the surface. CONTEJEAN (**3**), in speaking of the conditions in southwestern France, considers that his second belt of sea-shore vegetation, that is our middle and upper beach, is growing in a saline soil. MASCLEF (**9**) found the salt content in dunes near the sea to be 0.351 per cent., while at a distance 150^m from the shore he found 0.17 per cent. of sodium chlorid, and at 1500^m he discovered 0.041 per cent.

There has been some doubt, however, in the minds of certain authors whether the coastal dunes are impregnated with common salt or not. Among these is MASSART (**10**). The present writer has on various coasts made tests for salts in the sand by means of chemical analysis. The result of these observations shows that under ordinary circumstances *dunes do not contain sodium chlorids in perceptible*

quantities. When salt is found *it has been deposited as spray from the sea*, but this is rapidly washed out by rain water, and when no precipitation has fallen, the *sodium chlorid does not come into contact with the ground water but is detained on the surface by the upward movement of the water*. Because of this the roots of the plants are not exposed to sodium chlorid. On the littoral dune the uppermost half an inch layer of sand usually contains some salt, but deeper in the soil no salt is found before we reach the sea-level. The upper beach has very similar conditions, as a rule, except at times when inundated by high water. Even on the middle beach we cannot find that the sand would be impregnated with salt. On the contrary, for quite a considerable depth there is fresh water, which, on account of its being lighter than the salt water, flows on top of the latter. This fresh water is a part of the continuous stream of rain water, which slowly works its way to the sea. The roots of the plants do not, as a rule, penetrate deeper than to the bottom of this fresh-water layer, and it is therefore wrong to assume that the plants are growing in salt water on the beach. Even on the front beach, the layer in which the roots of the plants are situated has more of a brackish character, because the water from the beating waves runs off before it has time to sink through the layer of fresh water, which flows on the surface of the salty ground water.

On a superficial investigation of the beach it appears that the ground is thoroughly soaked with salt water, but careful sampling from various depths and subsequent analysis has made it apparent to the writer that this is not the case. It is a well-known fact, however, that the ash of strand and marine plants contains a much larger percentage of sodium chlorid than that of inland plants. This is due, of course, to the presence of a greater amount of salt on the sea shore than inland. But when it comes to a comparison between the conditions on sea shores and salt-impregnated formations in the interior, the amount of salt in the latter is much greater. This fact brings forward the question whether all sea-shore plants are halophiles or not. KEARNEY (**8**) has investigated this question and comes to the result that they are not. The present writer made numerous experiments in this direction and the results confirm those of KEARNEY, as the following discussion will show.

It has long ago been proved by experiments that most inland plants

are injured by the presence in the soil of sodium chlorid in certain quantities, which the strand plants are able to tolerate without evident injury. There appears to be a certain maximum amount of salt for every species, to which it is very accurately adapted, and this maximum cannot be overstepped without fatal results to the plant. In some cases investigated by the writer this maximum has been found to be:

	Per cent.		Per cent.
Argentina anserina	1.9	*Glaux maritima*	2.7
Aster Tripolium	2.6	*Juncus Gerardi*	2.2
Atripex hastata maritima	3.1	*Matricaria inodora maritima*	2.3
Cakile maritima	2.9	*Plantago maritima*	2.8
Crambe maritima	2.5	*Sonchus arvensis maritima*	2.6
Elymus arenarius	2.6	*Triglochin maritimum*	2.1
Erythraea vulgaris	1.9		

These experiments were conducted in the summer of 1894 with plants from the Baltic coasts. Sand cultures saturated with normal solution of sodium chlorid were used. In these cultures young seedlings as well as older plants were grown, and the results given above refer to seedlings, about two weeks old at the time of transplanting. They were grown in fresh water for five days, after which time the salt solutions were gradually applied. It was found that plants which had been growing on strands with low salinity were considerably more sensitive to an increase in the amount of salt than those which were brought in from the open shores with higher salt content in the water. Strong, well-developed plants adapted themselves more readily than weaker specimens to the gradual transfer to stronger salinity. It would be of considerable interest to ascertain whether this specific limit of salt concentration could be raised much higher by growing the plants through a succession of seasons. The ability of the seashore plants to endure salt in the soil without injury and by adapting themselves to these conditions has, no doubt, been the ultimate cause of their being in many cases confined to the strand, precluding competition from forms not possessing this power of resistance.

We also know from experimental cultures that strand plants do not need sodium chlorid in order to develop normally. The question then arises whether the common salt, even when present in quantities lower than the maximum, exercises a poisonous influence or not. SCHIMPER, who paid much attention to this matter, came to the con-

clusion that the chlorids produce abnormal conditions in the plants and disorders in the nutritive processes. In this regard most writers agree, but in explaining the means by which the plant neutralizes this injurious effect of common salt there is a wide divergence of opinion. While SCHIMPER maintains that the structural adaptations of halophile plants are caused by the necessity of keeping the relative amount of sodium chlorid in the cell-sap below the specific danger point, DIELS (**6**) considers that this is effected by chemical decomposition of the salt. This process is not known, but DIELS assumes that in respiration the succulent halophytes differ from other plants in that the oxidation does not proceed so far in halophytes, but stops at malic acid or some isomer, with which the cell-sap becomes saturated, while only small quantities of carbonic acid are evolved. The malic acid then combines with the hydrochloric acid and is excreted by the roots. BENECKE (**2**) has severely criticized these conclusions of DIELS.

In regions having a hot climate the evaporation of water is very great on the coastal sands and the salinity is naturally higher. The concentration of salts is also increased in countries where the rain falls only during a rainy period, leaving a long time in which no leaching of the salts takes place in the soil. In places with frequent rains the salts are rapidly washed out and carried deeper into the ground, until the lateral flow of water toward the sea is encountered.

The observations on salinity of strand sand made by the author are all based on chemical analysis. The electrical method of determining the salinity as employed by the United States Bureau of Soils was not familiar to the author at that time, but careful observations and determinations of the salinity with that method ought to reveal the causes of distribution of certain plants on the strand. The writer has found that *the small embryonic dunes formed by certain strand plants contain a greater amount of salts than those occupied by others.* Thus, for instance, the small, embryonic, *Elymus arenarius* dunes always contain 0.005–0.009 per cent. more sodium chlorid than the *Ammophila arenaria* dunes. Likewise the Mesembryanthemum dunes on the California coast have a higher salinity than the Abronia dunes, while the elevations formed by *Abronia latifolia* contain more salt than *A. umbellata* hummocks. These are the only examples which have been verified by analyses, but more extended investiga-

tions will, no doubt, give an explanation of certain hitherto unexplained features of the local distribution of strand plants.

We often find on sandy sea shores a number of immigrants from inland formations, and this occasional occurrence of plants which do not naturally belong to such habitat shows that it cannot be the chemical composition of the salt water that keeps so many island plants from the sea shore, but other adverse conditions, which allow only the peculiar sand-strand flora to develop. Even on the front beach, where the salinity is greatest, we cannot attribute the scarceness of the plants to the salt content, but to the easily movable sand soil.

As we have already mentioned, the lateral current of fresh water flowing on the surface of the salty ground water near the sea has to be taken into consideration when we discuss the salinity of the strand soil. Our assumption that the conditions of the strand are not such as to characterize this formation as halophytic is borne out by the analyses made of the salinity of the soil at different depths. Many true halophytes, of course, occur on the sea shore, but the strand flora as such must rather be classified as a halophile flora, while the true halophytes are those plants which are confined to saline situations in the interior, or where we know that the hydrodynamic conditions do not change to any marked degree the salinity, as is the case on the sea shore. If this holds good, the halophytes occurring on the strand must be regarded as immigrants from dry saline habitats.

Several Salsolaceous plants, widely spread in the interior of Australia, sometimes occur on the sea shores of that continent as straggling poor specimens, but reach their best development in the dry saline soil of the interior. SCHIMPER (13) maintains that the cliffs on the sea shore have a much less halophile flora than the sandy or marshy strands. This is evident to everyone who has studied the strand floras, but we shall find that the plants even on the cliffs exhibit many characters of the halophytes, and are sufficiently differentiated from the cliff vegetation of inland situations to warrant a classification as halophile. The physical nature of the substratum prevents its being impregnated with common salt. We have here to account for the development of adaptations so characteristic for halophytes, not so much through the influence of salt in the soil as through the salt

contained in the spray, to which the plants are constantly exposed. On sandy soils the protectional adaptations are caused more through the physical conditions of the sand, than through the salt content of the soil. The characteristic vegetation developed on all sand formations, inland as well as on the coast, is so much alike, that there is no reason to assume that the sodium chlorid content of the sea shore, which in fact is not very large, would be responsible for the aspect of the vegetation on marine sand strands. On coastal marshes the conditions are different, and this is also evident in the vegetation on such formations, which in no way differs from that on saline marshes in the interior, and always is composed of true halophytes.

A series of samples of the soil was taken with earth-auger on the beach and dunes at Fremantle, Western Australia, at various depths, and subsequently examined for soluble salts. The results appear in Table XI.

TABLE XI

Date	Formation	Distance from high-tide mark in meters	Character of soil	Depth in cm.	Angle of slope	Temperature ° C.	Degree of moisture 1–10	Percentage of salt	Notes
Dec. 18, '02	Lower beach, upper limit	2	Medium sand	20	15	18	9	0.005	
	Middle beach	5	Medium sand	35	21	20	6	0.004	Sparse vegetation
	Border of middle and upper beach	7	Coarse sand	30	23	20	6	0.004	
	Upper beach	10	Medium sand	30	26	22	4	0.009	
	Dune inside littoral dune	28	Fine sand	40	10	23	5	0.003	
	Littoral dune	15	Fine sand	40	30	21	4	0.007	
	Dune marsh inside littoral dune	29	Finest sand	20	0	19	10	0.005	
Dec. 21, '02	Middle beach	8	Medium sand	25	8	14	4	0.006	
	Same place	8	Medium sand	50	8	12	3	0.004	
	Upper beach	14	Medium sand	25 50	15	16 15	3 5	0.011 0.006	Sparse vegetation

DEVELOPMENT OF HUMUS.—There is no other soil which so little favors development of humus as the loose shifting sand. The organic substances that happen to be deposited on the sand are very rapidly decomposed by the admission of air, and the physical structure of the sand allows rain water to percolate and thus to carry the fine humus particles deep into the soil and out of reach of the roots. The earthworms, which are the most active agents in mold formation in forests, as DARWIN and MUELLER have shown, are entirely absent in sand and the mycorhizal fungi seem not to thrive on the beach, where they are likely to be exposed to occasional contact with sodium chlorid.

When a shrubby vegetation has got a foothold on the sand, the humus is developed to the best advantage. In the shade of the bushes remains of plants do not decompose so easily as on the open ground, they are more sheltered from the rain, and an accumulation of humus can take place, so that grasses and herbs are able to get a footing. When this has happened the sand is usually made permanently stable. The few animal remains that are thrown up on the front or middle beach enrich the soil on these formations only temporarily, and do not play any important rôle in the formation of the humus on the sand.

Topographic factors

The topography as a factor influencing the development of vegetation is very often overlooked by writers on plant geography. Its importance, however, is so considerable that it cannot be omitted in a discussion of the agents which exert their influence on plant life. On the vegetation topography acts principally indirectly, by determining to a great extent the moisture content of the soil, by influencing the temperature, the exposure to winds, and also the light relations. We intend here to mention briefly only the principal features of topography as far as they influence the conditions on coastal sand formations.

SURROUNDINGS.—From our previous discussion (**11**) of the development of the various sand formations it is apparent that the surroundings are of the greatest consequence to the evolution of dunes. On many of the coasts investigated the topographical conditions have been of such character as to prevent any greater development of dunes. Such was the case, for instance, on the southern shore of the

Gulf of Finland, where almost the whole shore line consists of a steep wall of rock, leaving only a narrow strip of beach along the water edge. In places where this rocky barrier was broken and the winds are allowed free play over a wider stretch of land, dunes appeared at once. The vegetation on the beach of the former type presents a somewhat different aspect from that on open shores with the background of a dune-complex. The best evidence of the influence of surroundings on the composition of the vegetation can be seen if we compare that on a sand field and on a dune-complex with its diversified topography. Also on the slopes of an unbroken dune, the vegetation is usually quite different from that on a train of dunes frequently cut through by furrows and valleys.

On beaches a similar difference can be noticed, and the cause underlying this effect can only be attributed to the topography. Where we have a long continuous beach the plants associate according to rules different from those which have determined the composition of the communities on cuspate forelands. This was especially evident on the shore stretches of sandy beaches that are so common on the shores of the islands in the Baltic.

ELEVATION.—This factor is of minor importance in regard to the sand-strand vegetation. The sand formations do not rise to any great height, but it seems that certain plants choose their place of growth with reference to altitude, even on these formations. Without taking into account the fact that humus naturally accumulates more rapidly in the depressions, we find that some plants prefer the foot of a dune, while others are found only on the middle of the front slope, and others again do not thrive except on the top of the dune, where they are constantly being covered with drifting sand.

On the beach a corresponding selection of habitat takes place. Some plants never occur on a low beach although the conditions otherwise seem to be favorable, but only a short distance away, where the beach rises more abruptly, they appear again. We have presumably two different causes for this. While on the dunes the selection of a place of growth is determined apparently by the plant's greater or less power of resistance against the drifting sand, on the beach the dominant cause must be the sensitiveness of the plant to inundations of salt water.

Depressions between the dunes offer to many plants a refuge from the sand-laden winds, and the richer soil in the troughs induces other plants to settle.

GRADE OF SLOPE.—We have elsewhere (11) referred to this factor as being of great moment in the growth of dunes and in the development of sand formations generally. Its influence on the moisture conditions is of no less importance. The higher up on the slope the drier is the soil, the greater the evaporation, and the more intense the influence of the wind.

The exposure of the slope is another matter of the greatest consequence to the vegetation on the sand formations. The various degrees of slope ought always to be considered when a description of a habitat is given in order to arrive at a correct understanding of the conditions that have determined the composition of the plant community. Southern slopes in the northern hemisphere and northerly slopes in the southern are drier than those facing other directions, and the vegetation has a corresponding aspect. On sea coasts the exposure to the prevailing winds has to be noticed.

Light relations are further to a certain degree determined by the direction of the slope, and this is of special importance in northern latitudes, where light even during the period of growth is not too abundant.

Historical factors

Under this heading we include all those factors whose influence on plant life is determined by time. This must not be understood as if time was not involved in the action of other factors, but that the period of influence and the time required for attaining any results is of such a long duration, that it cannot be ascertained within a few generations of plants. Physiographical changes of land and sea, whether within a century or within long geological periods, have to be considered in this connection. One of the most important historical factors to be looked upon in explaining the present conditions on sand strands is the oscillation of the coast line. The erosion of the shore by waves and the deposition of sand or other material are equally important. Sand deposits are in many places formed so rapidly that the effect can be noticed within a very short time. The influence of animals, principally through grazing, and the interven-

tion of man belong strictly to the group of biotic factors, but have here been considered in connection with the historical factors as a matter of convenience.

OSCILLATION OF THE COAST LINE.—Many coasts are slowly rising, while in other instances the coasts are sinking. We have excellent examples of both kinds of movements on the Baltic. While the whole coast of Sweden north of Stockholm, and the coasts of Finland are in a state of elevation, the southern shore of the Baltic is in a corresponding state of depression. Besides having a great influence on the development of dunes, this oscillation of the coast line has had a marked bearing on the evolution of the flora on the coastal sands.

On the shores mentioned which are rising, one may see in some instances how long stretches of land are slowly raised above water and in a few years carry a cover of vegetation that gives an instructive demonstration of the successive stages of development of the plant associations. Again, on the sinking shores of the southern Baltic may be frequently found examples of plant communities being destroyed in the course of a few years through the submersion of the shore.

On the coasts bordering upon the oceans oscillations also take place, but they are usually neither so regular nor so rapid as these changes on the Baltic.

In postglacial times considerable changes of the coast line of the Scandinavian countries have taken place, and as we are able to follow these changes with the assistance of fossil remains of plants, found in old sea beaches now raised high above the present level of the sea, we can to some extent interpret the various stages of development which have been passed before the flora arrived at its present state. This question will be discussed in another paper.

EOLIAN DEPOSITS.—The influence of the wind on formation of plant communities on the coastal sands is shown not only in the peculiar arrangement of the plants in patches, but also in the aspect of the aggregations of plants, which (especially in the case of trees and shrubs) give evidence of being continuously attacked by the strong winds laden with spray or sand. Shrub associations on open strands are usually lower toward the shore, gradually increasing in height inland under the shelter of the more exposed specimens.

Most of the sand-strand plants are not able to withstand partial burying by the shifting sand; consequently it very often happens that

FIG. 1.—*Cupressus macrocarpa* on Cypress Point, Monterey, Cal., showing influence of wind. (Photograph by author.)

FIG. 2.—Rejuvenated Salix dune at San Francisco, Cal. (Photograph by author.)

whole communities are suddenly destroyed and their place taken up by plants able to endure more or less complete covering by sand. Sometimes it may be observed that trees, which are being buried by

an encroaching dune, are bent leeward (*fig. 1*). The cause of this is to be found in the continuous pressure, or in sudden gusts of wind which bend the trees while the onrushing sand prevents return to the original position. As a rule the sand on the lee side of a dune is moister, and the slope is consequently steeper. Often slides of sand take place, and they also bend or even break the trunks of the trees.

Dunes which have been made stable by a cover of plants are sometimes again broken up by the wind (*fig. 2*). Such formations are often met with on the Baltic coasts. On these broken-up dunes the usual series of development of vegetation begins anew and thus

FIG. 3.—Embryonic dunes inland from littoral dune, south of Cliff House, San Francisco, Cal. (Photograph by author.)

they have a peculiar character, remnants of the old communities being mixed with the new immigrants. A new life-history of the plant community is started, and during the course of development it may take a direction entirely different from the former series.

Vegetation covering on the ground will greatly slacken the speed of the air current which comes into immediate contact with the ground, and if bushes or other obstructions are in the path of the wind, dunes are often formed behind them (*fig. 3*). The plants that are first struck by the whole force of the wind are mostly injured, not only by its mechanical action, but to a greater extent

by the sand carried by the wind. While the wind in itself dries the plant, the sand particles, which often have a high temperature, are still more apt to increase the evaporation, and thus to hinder the development of the plant (*fig. 4*). Further, stems of plants growing on exposed places on coastal sands are often eroded by the sand, and even the green leaves are sometimes cut into shreds during severe storms by the sharp angular sand grains.

FIG. 4.—Effect of wind on *Leptospermum scoparium* Forst. on dunes at New Brighton, Canterbury, New Zealand. (Photograph by Dr. L. COCKAYNE.)

OTHER SEDIMENTS.—As we have pointed out in another place sand is especially likely to accumulate in the neighborhood of river mouths, and in such places heavy floods often carry down and deposit on the sand considerable quantities of mud, which then enrich the soil, and cause the appearance of a quite new flora, that soon will exclude the true sand plants.

On almost all marine coasts quantities of seaweeds are thrown ashore by the waves, but in warm climates they are so rapidly decomposed and the remains washed away, that no accumulations can be

effected. In more temperate regions, however, these seaweeds lie in banks on the beach for some time, and add to the fertility of the

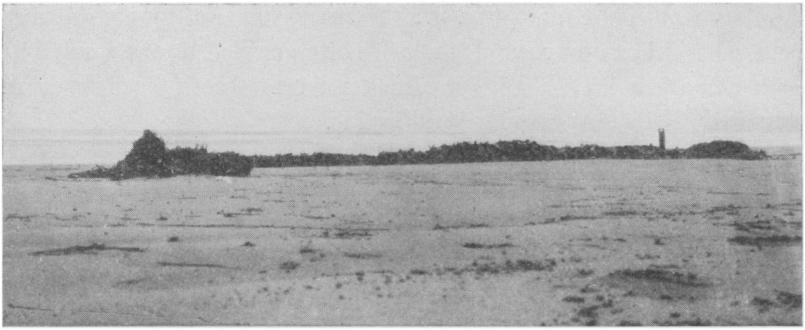

FIG. 5.—Bank of Macrocystis on the beach at New Brighton, Canterbury, east coast of South Island of New Zealand. Height of scale 41 cm. (Photograph by Dr. L. COCKAYNE.)

FIG. 6.—Kelp banks on West Australian coast. (Photograph by author.)

soil. *Figs. 5* and *6* show such kelp banks from the coasts of New Zealand and West Australia.

Along the shores of the Baltic a considerable amount of seaweeds,

principally *Fucus vesiculosus*, is deposited on the beach at high-water mark. On open shores these banks mark the limit of vegetation toward the sea, and are characterized by a vegetation quite different from that on the rest of the beach.

MAN'S INTERVENTION.—The principal influence of man on coastal sand floras is a result of his endeavors to arrest the drifting of sand. This is mainly done by planting so-called sand-binding plants, or by covering the loose sand with refuse or other material. Either action brings about a considerable change in the natural development of the sand vegetation.

Near cities the sand dunes are sometimes used for supplying sand for industrial purposes, and in such cases the removal of the sand will naturally change the conditions for the original vegetation. Fires are sometimes started through the carelessness of man, but as the natural vegetation is very seldom dense, the influence of fires on sand formations on the coast is not great, except in artificial plantations.

Grazing animals do more injury to the sand vegetation by trampling and uprooting the plants than by actual feeding on them, and in the neighborhood of many cities, where sandy beaches and dunes occur, human agency is equally detrimental to the plant covering.

Summary

Summing up the physical conditions prevailing on the various sand formations on marine coasts we would say that *the submerged beach* is always covered with water, and therefore is the most salty of all the formations. The soil is loose, the temperature that of the sea water, and the surf is continuously beating. The vegetation is therefore especially adapted to these conditions, and in most cases no plants at all are able to gain a footing on this formation.

The front beach is periodically washed by the waves, presenting alternating terrestrial and aquatic conditions. It is almost constantly exposed to the spray and has a salty ground not very deep under the surface. The soil is very loose, still more so than on the submerged beach. Strong insolation, rapid evaporation, and a constantly changing temperature are characteristic. It is on account of these adverse conditions usually devoid of vegetation, with the exception of a few unicellular algae, often Cyanophyceae, but where

the formation has not been inundated for a few days only the spores of the algae retain their vitality. On the Baltic coasts where the salinity of the sea water is low, conditions approach more or less those on fresh-water shores, and many green algae occur in the sand. The width of the barren front strand varies not only with the slope, but also with the force of the surf.

When a higher vegetation occurs on this formation it is open and

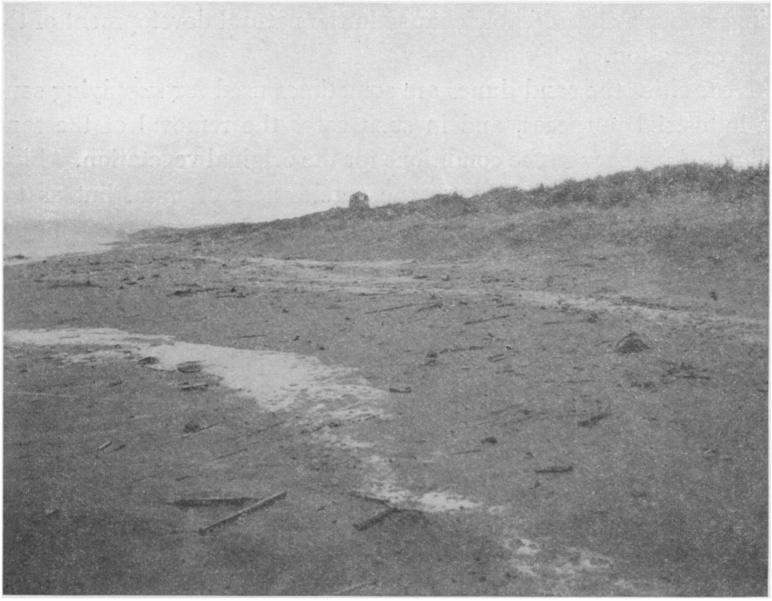

FIG. 7.—Middle and upper beach south of Cliff House, San Francisco, Cal. On upper beach small dunes made by *Cakile americana*. In background littoral dune with Ammophila. (Photograph by author.)

very poor. The loose soil, the wind, and the impact of the surf place a limit on the types that are able to develop. These are mainly annuals or perennials with long creeping rhizomes and the flora is always poor both in species and individuals.

The middle beach is characterized by its light color, its abundant moisture, its low salinity, its loose soil, and its comparatively low temperature. Occasional inundations, spray, and wind are the direct causes of the scattered vegetation, consisting mainly of annuals

or a few perennials. These plants also are more or less dwarfed, because of the wind and the cold substratum. The tension line between this and the following formation is very marked. Some-

FIG. 8.—Ammophila dunes at San Francisco, Cal. Embryonic Salix dune to the left. In winter. (Photograph by author.)

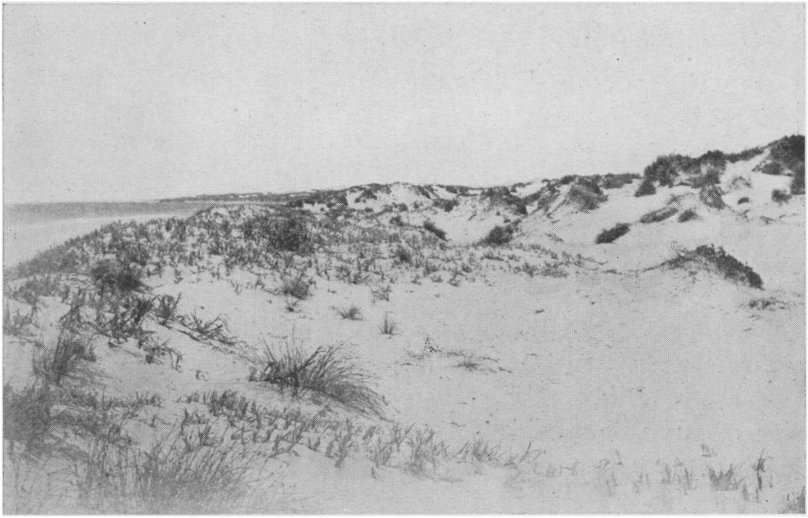

FIG. 9.—Grassy littoral dune, north of Fremantle, Western Australia. (Photograph by author.)

times a transition belt can be distinguished, marked by a darker strip of humus-mixed sand, and covered with a denser vegetation (*fig. 7*).

The upper beach has a higher percentage of humus, abundant moisture, and a higher temperature than the middle beach. The illumination is much greater, especially during certain times of the day, when the formation is not shaded by the littoral dune. Evaporation and radiation from the soil, however, are less intense, because the

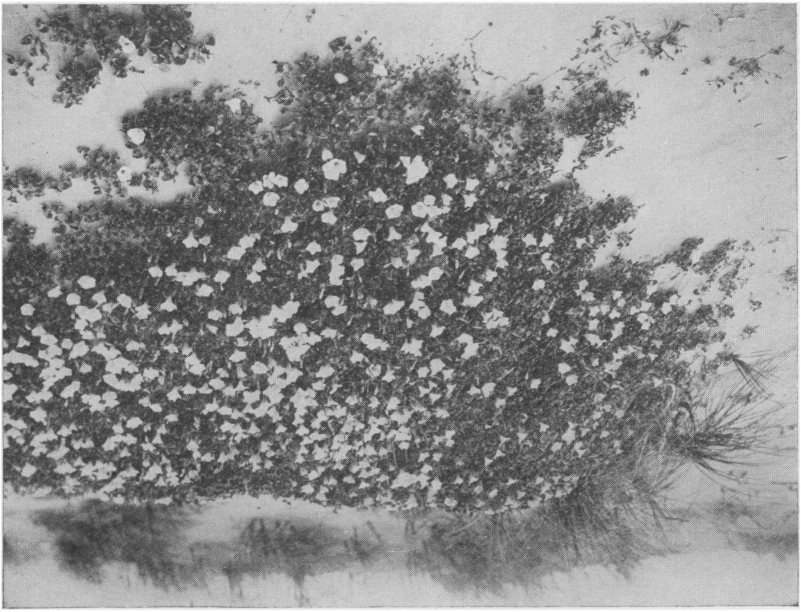

FIG. 10.—Soldanella community on dune slope at New Brighton, Canterbury, New Zealand. On summit, *Scirpus frondosus*. (Photograph by Dr. L. COCKAYNE.)

ground is well covered with plants. The amount of spray is less the farther we go from shore, and complete inundations occur only at very long intervals. The distance to the salty ground water is considerably greater than on the lower formations, and very few true halophytes appear on this belt. The influence of wind is very marked in that sand is blown from the middle beach over this formation, which often is covered with small embryonic dunes (*fig. 8*). The wind favors transportation of seeds and shoots from the middle

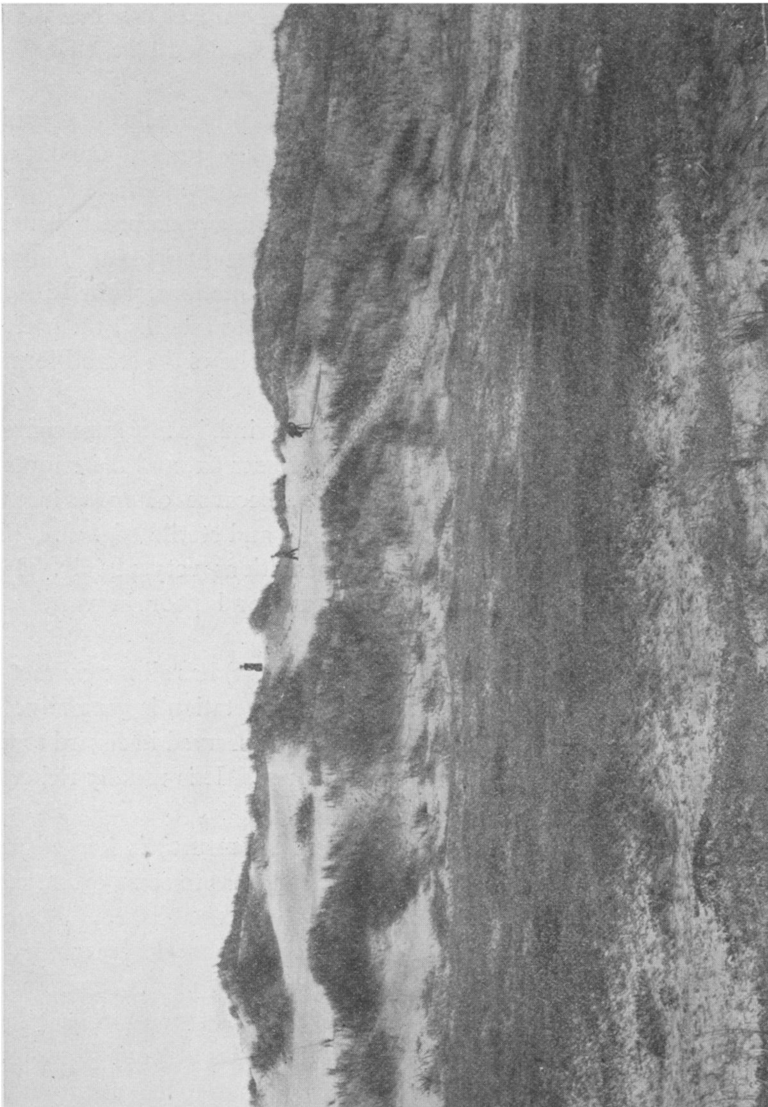

FIG. 11.—Sand dunes at Studeli Mile in north Jutland, Denmark, covered by *Elymus arenarius*, *Ammophila arenaria*, *Carex arenaria*, etc. In the foreground especially *Salix repens*. (Photograph by Dr. F. BÖRGESEN.)

beach, and in many cases the occurrence on the upper beach of plants belonging to the middle beach can only be explained by their having been blown landward from the original position.

The vegetation on the upper beach consists principally of perennial herbs, shrubs, or low trees. The tension line toward the littoral dune is not so marked as in the direction of the middle beach, but where no dune formations are developed the upper beach usually borders upon a forest. In the latter case it often happens that inland plants have wandered out to the sea-shore formations, while it never happens that sea-shore plants have been able to establish themselves inland on the meadow or forest that usually follows the strand formations.

The littoral dune is much exposed to the wind, its moisture content is low, constant oxidation of organic water goes on, and the temperature is lower than on the upper beach, because of more intense radiation. The soil is very loose, shifting, and sterile (*fig. 9*). The vegetation shows the results of these conditions very plainly. It is prostrate and dwarfed in habit, scattered and poor in variety of forms.

The active dune (the white dune of WARMING) has all the characteristics of the littoral dune in excess, and its vegetation is generally still more monotonous. Some difference can be observed in regard to the plants on the slope and summit of the dunes. It is usually richer in species on the latter part of the formation.

The stationary dune (the gray dune of WARMING) is formed at a greater distance from the sea, where the sand has to some extent consolidated, and a heather vegetation has been established. Formation of humus goes on, the plants grow closer and closer, mosses or lichens occupy the ground between the higher plants, and finally the soil is completely covered with a carpet of vegetation. This heather association is the final stage in the series of sand-plant communities beginning on the small embryonic dunes to leeward from the littoral dune (*fig. 11*).

The sandy field is richer in humus than any of the former sand formations mentioned. It has a comparatively level surface, is better able to retain moisture, and has a higher temperature. The sand grains are of such uniform size as to prevent ripple or dune formation, and

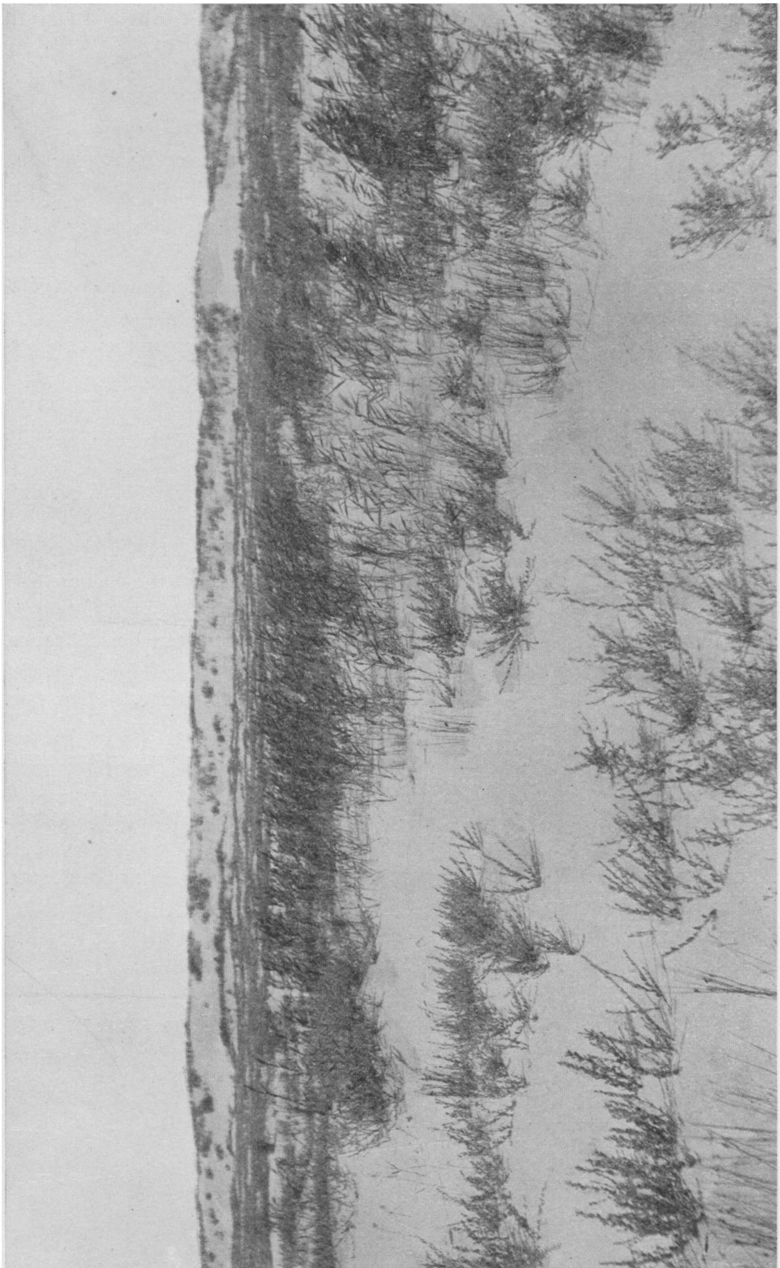

FIG. 12.—Sand field at Lodskovvad Mile in north Jutland, Denmark. The place was formerly a shallow lake, which had been filled in with sand three years previous to the time (August 18, 1898) when the picture was taken. The vegetation consists of *Salix repens*, *Juncus balticus*, *Agrostis alba maritima*, *Eleocharis palustris*, and *Phragmites communis*. In the background sand dunes with Elymus and Ammophila. (Photograph by Dr. F. BÖRGESEN.)

the vegetation covering is consequently developed in quite a different way from that on dunes (*fig. 12*).

MEXICO, D. F.

LITERATURE CITED

1. BANG, J. P. F., Om de nord- og vestjydske Klitters Beplantning. Tidssk. for Skovbrug, Kjöbenhavn **12**:—. 1889.
2. BENECKE, W., Ueber die Diels'sche Lehre von der Entchlorung der Halophyten. Jahrb. Wiss. Bot. **32**:179–196. 1901.
3. CONTEJEAN, C., Géographie botanique. Influence du terrain sur la végétation. Paris. 1881.
4. COOKE, W. E., The climate of Western Australia from meteorological observations made during the years 1876–1899. Perth. 1901.
5. COUPIN, H., Sur la toxicité des composés du sodium, du potassium et de l'ammonium à l'égard des végétaux supérieurs. Rev. Gén. Bot. **12**:177. 1900.
6. DIELS, L., Stoffwechsel und Struktur der Halophyten. Jahrb. Wiss. Bot. **32**:309–322. 1898.
7. HANN, J., Handbuch der Klimatologie. Stuttgart. 1897.
8. KEARNEY, T. H., Are plants of sea-beaches and dunes true halophytes? BOT. GAZETTE **37**:424–436. 1904.
9. MASCLEF, A., Études sur la géographie botanique du nord de la France. Journ. de Bot. **2**:177. 1888.
10. MASSART, J., La biologie de la végétation sur le littoral Belge. Mém. Soc. Roy. Bot. Belgique **32**:7–43. 1893.
11. OLSSON-SEFFER, PEHR, Relation of wind to topography of coastal drift sands. Journ. Geol. **16**:549–564. 1908.
12. ———, Hydrodynamic factors influencing plant life on sandy sea shores. New Phytologist (in press).
13. SCHIMPER, A. F. W., Pflanzengeographie auf physiologischer Grundlage. Jena. 1898.
14. WARMING, E., Plantesamfund, Grundtraek af den oekologiske Plantegeografi. Kjöbenhavn. 1895.